

# THE ORIGIN OF THE LOOP IN ARTICULATE BRACHIOPODS

by A. WILLIAMS and A. D. WRIGHT

**ABSTRACT.** The lophophore of living articulate brachiopods develops from a pair of generative zones which are first located antero-medially of the mouth, and are each responsible for the proliferation initially of a single set of filaments, constituting the trocholophe, and subsequently of a paired set of filaments. Brachial supports are secreted within sheaths of outer epithelium and grow independently of the lophophore, but those developed in shells about 1 mm. in length invariably support a simple, subcircular lophophore; and since the earliest known loop, that of the spiriferoid *Protozyga*, was fully developed in sexually mature shells of that size, it probably appeared coenogenetically in a neotenus stock. The modal size of the earliest terebratuloid loops compares with that of the primary coils posterior of the jugum in contemporary spiriferoids, so that the terebratuloids could have been derived neotenusly out of the spiriferoids. The loop of the pentameroid *Enantiosphen* is only superficially comparable with the centronellaceid one, but that found in the dalmanellaceid *Tropidoleptus* is a remarkable homeomorph of the terebratuloid loop and probably differed only in the style of lophophore it supported.

## INTRODUCTION

THE presence of a calcareous loop in the brachial valve of an articulate brachiopod is usually taken to be diagnostic of a terebratuloid or a young spiriferoid shell and the structure is known, or is assumed, to have given support to the lophophore suspended within the brachial cavity. This type of skeletal support appeared rather late in brachiopod evolution, for the earliest known loop bearer, the spiriferoid *Protozyga*, is first recorded from the Middle Ordovician. Nevertheless, it has since undergone a remarkable series of changes, some of them so complicated that they are only intelligible if a number of assumptions about the original growth and disposition of the lophophore are adopted. With this end in view one of us (Williams 1956, pp. 260-72) used some generalizations derived from a study of living material to speculate on the nature of the lophophore in various extinct fossil groups. In 1959 four studies of this aspect of brachiopod morphology were published: two by Dr. D. Atkins on the development of the lophophores of *Platidia* and *Macandrevia*, a systematic study of some recent articulate brachiopods by Dr. H. M. Muir-Wood, and also a general account of the phylum by Dr. L. Hyman. All three authors were critical of some of the conclusions reached in 1956, but since their own interpretations either contradict one another or are, with one exception, unacceptable to any one familiar with the growth of the loop and the lophophore, some reappraisal of the present state of knowledge is necessary.

In addition it has long been known that two Devonian loop-bearing brachiopods, *Enantiosphen* Whidborne and *Tropidoleptus* Hall, are characterized by other morphological features which are typical, not of the terebratuloids or the spiriferoids, but of the pentameraceids and dalmanellaceids, respectively. The two stocks are all the more perplexing in that their restricted ranges coincided with the time when the terebratuloids first became common and widespread members of the Palaeozoic shelly faunas, a contemporaneity which had prompted the original authors of the genera to suggest that they were really aberrant terebratuloids. Through the kindness of Mr. A. G. Brighton of the Sedgwick Museum, Cambridge, and Dr. G. A. Cooper of the U.S. National Museum, it

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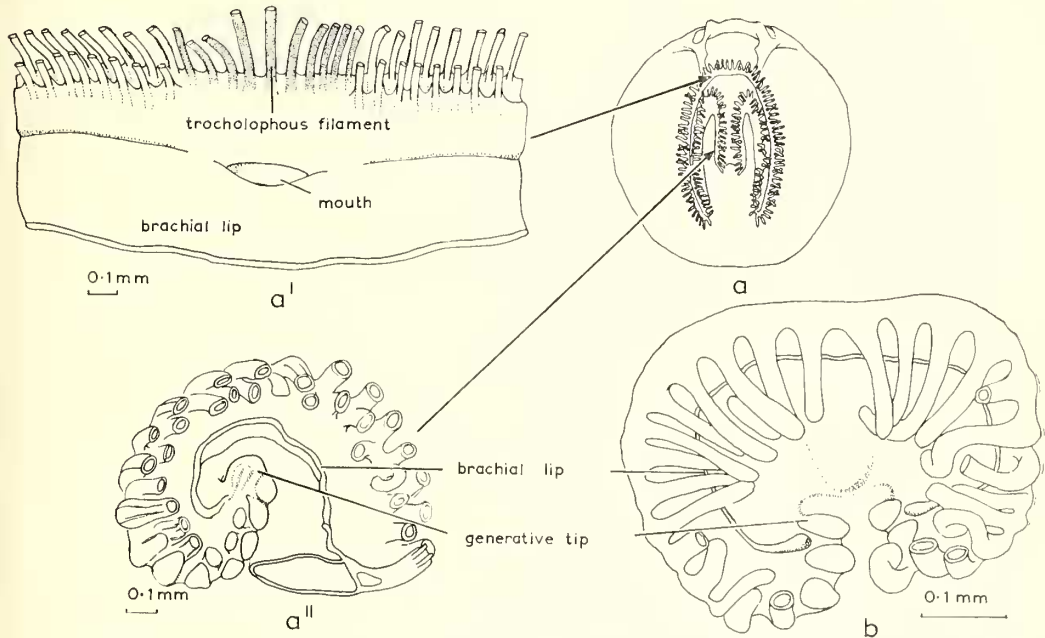
has been possible to serial section specimens of both genera and thereby conduct a detailed examination of the growth of all features in an effort to resolve any doubts about their systematic status, and to find out if their brachidial skeletons were indeed comparable in function and origin with those of contemporary terebratuloids.

#### THE RELATIONSHIP BETWEEN THE LOPHOPHORE AND THE LOOP IN RECENT BRACHIOPODS

In 1897 Beecher described the formation of the lophophore in living brachiopods as beginning with a proliferation of filaments to form a complete ring, the trocholophe, around an oral disk bearing a subcentral mouth. The trocholophe then becomes indented antero- or dorso-medianly (the schizolophous stage) and further growth of the lophophore results in a distortion of the original circle into a pair of spires (the spirolophe) or variably developed loops (ptychlophe) including a pair of long lateral ones (the side arms of the zygo-lophe) which are commonly associated with a pair of median coils to form a plectolophe. It is important to realize that Beecher (p. 105) took the formation of filaments in the inarticulate *Glottidia* as being representative of the earliest stages of growth for all brachiopods. At that time observations made by various authors on the early development of the lophophore of certain articulate genera, as well as Beecher's own investigations, appeared to confirm his assumption. In *Glottidia* (Brooks 1879) and also in *Lingula* according to Yatsu (1902), new filaments are budded off from either side of a lobe situated dorso-medianly of the mouth. This proliferation of new filaments from a median zone is responsible for the migration of the first formed pair along two curved arcs which meet ventro-medianly to form the completed trocholophous circle. In 1944 Percival (p. 13) described the growth of the lophophore in *Terebratella inconspicua* (J. de C. Sowerby) in an entirely different way. According to him the first pair of filaments arise ventro- or postero-medianly of the mouth and additional filaments grow in pairs one on either side of the earlier formed filaments. This pattern of growth, in contrast to that described by Beecher, involves a pair of generative zones expanding outwards from the median line to surround the mouth and then to meet dorso- and antero-medianly. The schizolophous stage now becomes intelligible in that it represents that phase of development in which these two generative zones first meet medianly. Further growth is, of course, responsible for a distortion of the initial, encircling disposition of the filaments. The arrangement of filaments observed by Percival has been confirmed by Atkins (1959*b*, p. 336) for *Macandrevia*, and judging from the early schizolophous stages of *Terebratulina* and *Tegulorhynchia* (text-fig. 1*b*) re-examined by us, it is feasible to assume that this style of development is typical of the articulate brachiopods. Whether it represents an invariable deviation from the development of the inarticulates remains to be seen.

In his account of lophophore development, Percival recorded that when eight pairs of filaments have been formed 'there is a rapid extension of the anterior border of the mouth, between the latest filaments, without a corresponding increase in the diameter of the opening'. Williams (1956, p. 260) interpreted the resultant flap over the mouth as the brachial fold or lip of the food groove, but Atkins (1959*a*, p. 106 and 1959*b*, p. 337) found that in *Platidia* and *Macandrevia* the lip first becomes differentiated antero-medianly of the mouth and thence spreads laterally towards the antero-median portion of the trocholophe. The difference is important because in these two genera at least the con-

verging tips responsible for the generation of filaments are not effectively separated from each other by the growth of the brachial lip. Atkins therefore concluded that, in the absence of this invagination from her growth series and also in the presence of a closed lophophoral ridge forming the base of the filament circle, the trocholophe was, after all, a complete ring as defined by Beecher. This is a repudiation of the suggestion by Williams (1956, p. 261) that, in the light of Percival's finding, the trocholophe 'is in reality a crescent capable of accelerated and differential growth at the tips of the antero-median



TEXT-FIG. 1. The plectolophe of *Terebratulina* (a) with enlargements to show the arrangement of the trocholophous filaments posterior of the mouth (a') and one of the median generative zones (a'') and the early schizolophe of *Tegulorhynchia* (b).

horns'. Certainly the lophophores of *Platidia* and *Macandrevia* pass, during development, through a phase morphologically comparable with a closed ring. But the growth of the trocholophe involves a migration of a pair of generative zones, responsible for the proliferation of filaments, from a ventro-median position to a dorso- or antero-median one and it is surely reasonable to conclude that the pair of dorso-median generative zones identified by Williams (1956, p. 261) as typical of the early schizolophous stage and also described by Atkins (1959a, p. 107, 1959b, p. 337) in the schizolophes of *Platidia* and *Macandrevia* are the same as the migratory ones of the trocholophe. In effect, the indentation which defines the schizolophous stages of Beecher represents the confluence of two growing tips, which tend thereafter to curl back upon themselves, and not a division of the lophophore into two lobes of growth subsequent to an initial expansion in an opposite direction (Beecher 1897, p. 108). In any case the trocholophous stage is at present arbitrarily defined because it ends with the first suggestions of an antero-median indentation corresponding to the beginnings of introversion of the two contiguous



growing tips. The schizolophous stage, however, as understood by most students of the phylum is practically coincident with a marked change in the disposition of filaments (text-fig. 1a). In the initial stages of filament proliferation up to the encirclement of the oral disk and the start of introversion, the filaments occur singly, but thereafter they bud off in pairs, slightly in echelon, but effectively forming an outer and inner set arising from each generative zone. Many authors have commented on this fact and have noted that in adult lophophores those arranged in a single row have been pushed back to form the postero-median margin of the mouth. These are, of course, the first formed filaments and their disposition in both the larval and adult stages of growth so conveniently distinguishes them from the double series which arise during schizolophous stages of growth that we consider it preferable to define the trocholophe in terms of the filaments rather than in terms of a completed circle. The fully developed trocholophe of articulate brachiopods then may be described as *that growth stage of the lophophore where primary filaments, arranged in a single series surrounding the oral disk, have budded off from a pair of migratory generative zones which are now contiguous antero-medianly and are about to give rise to two paired series of filaments.*

The onset of paired filaments may be slightly delayed or accelerated during the development of the lophophore. Percival described the invagination of the anterior border which gives rise to the brachial fold as occurring when about sixteen filaments surround the oral disk. Fifteen or sixteen single filaments have been counted postero-medianly of the mouths of four adult *Terebratella inconspicua*, so that according to our definition the invagination corresponds to the beginning of the schizolophous stage. In a similar manner the end of the trocholophous stage occurred in the early schizolophous specimen of *Platidia davidsoni* (E. Deslongchamps) figured by Atkins (1959a, p. 107, fig. 2) when the formation of thirty-six or thirty-seven single filaments had been completed and in *Macandrevia cranium* (Müller) when about twenty-four filaments had appeared (Atkins 1959b, p. 338). According to Atkins a slight indentation and interruption of the lophophoral ridge of this latter species occurs at the twenty-four filament stage and one or more pairs of buds are present in place of the *asymmetrical* bud which marks the end of the trocholophous stage as interpreted by her and Beecher. This asymmetry of growth is due, as Percival noted (1944, p. 13), to a slightly staggered appearance of the filaments during their spread from the postero-median region and confirms the presence of two generative zones in place of a single antero-median one as described by Beecher. The number of primary filaments arising in the trocholophous stage is only slightly variable for the species and probably even for the genus: in a small sample of adults of *Terebratulina* sp. from Crinan Loch, 8, 9, 10, 11, and 12 primary filaments were present postero-medianly of the mouth in 1, 0, 7, 1, and 2 specimens respectively.

In describing more advanced stages of lophophore growth, Williams (1956, p. 263), guided mainly by the enlargement of the skeletal support, supposed that a pair of secondary generative zones become active antero-laterally of the primary median zones to give rise to the side arms of the zygolophe and plectolophe. Atkins (1959b, p. 348) points out that if such zones existed proliferation of filaments should occur at the apices of the side arms. Filament buds, however, are found only in the primary median zones and any increase in the number of filaments on the side arms can only be accounted for by their migration from the median coils. The growth of the side arms need not involve the production of new filaments but simply an expansion of tissue relative to the rest of



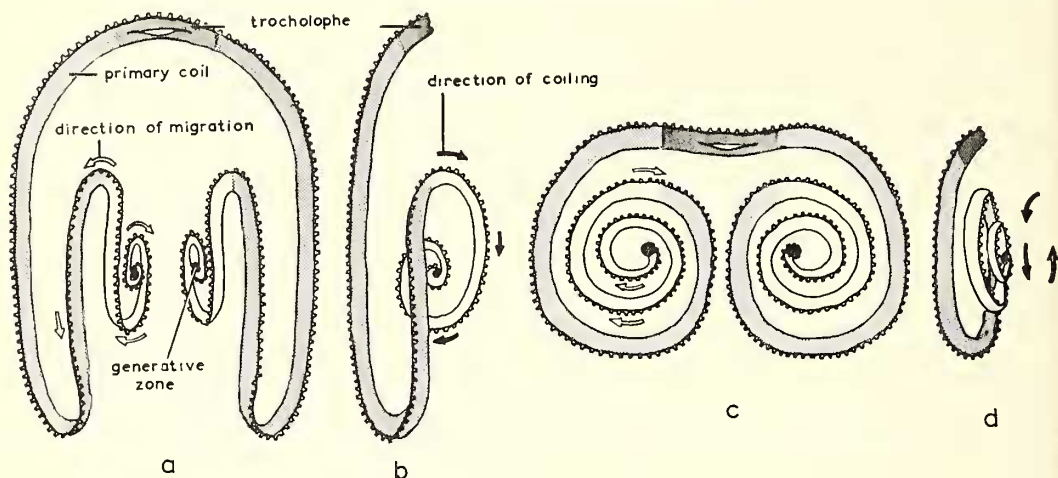
the lophophore, and this does take place. In eleven brachial valves of *Terebratulina sp.*, between 8 and 10 mm. long, counts of filaments were obtained for standard lengths of the lophophore antero-lateral of the crura, immediately posterior to the apical curve of the side arms and also along the middle part of the outermost coil. The incidence of filaments per unit length on the side arm was on an average 74 per cent. and 82 per cent. the counts of those on the coil and the crural region, respectively. But this increase in overall size does not account for the entire elongation of the side arms, and, since the number of filaments along them does increase with age, the chief contribution to their forward expansion must be due to the addition of filaments from the median coils in the manner described by Atkins.

The migration of filaments outwards from a pair of generative zones towards two points, beyond which no further relative movement is possible (initially represented by the ends of an extended trocholophe), makes the definition of 'zones of transit' necessary, because they may be responsible for the ultimate disposition of the lophophore. As far as we can judge, the only method of determining when a filament becomes incorporated into the non-migratory part of the lophophore is by studying the transit of certain marked filaments in living material, an experiment which is beyond our present resources. In the meantime it seems reasonable to conjecture that migration ceases just lateral of the zones of maximum distortion of the initially circular outline of the lophophore. In the terebratuloids these are the side arms and it is quite possible that the posterior part of the lophophore together with the descending portions of the side arms (excluding their apices) represent the non-migratory zones, and that the apices and the ascending portions of the side arms, as well as the median coils, consist of filaments in transit.

The fact that such unlike brachial arrangements as the spirolophe and the plectolophe are derived from similar, early schizolophes with medianly placed generative zones leads to some understanding of how these diverse patterns arise. In comparative terms the side arms and the median coils of the terebratuloids are equivalent to the first formed coil and the apical spires, respectively, of the rhynchonelloid arms (text-fig. 2). Some confusion exists over this rather obvious homology. Hyman (1959, p. 548) states that in the spirolophe of inarticulates and rhynchonelloids 'the median arm [i.e. the median coils of the plectolophe] is wanting and the two lateral arms elongated still further and coiled into helicoidal spires'. This misinterpretation is later (p. 550) repeated in the assertion that 'the structure [that is of the spirolophous arm] is the same as that of half of a plectolophous arm'. Muir-Wood (1959, p. 310) contends that the paired growing regions of the trocholophe are represented by the side arms of the plectolophe 'while the median coil is developed from the region anterior to the mouth' (caption to her text-fig. 4a-c, which is a reproduction of immature lophophores of *Terebratulina* from Morse 1871). The implication again is that the side arms are the homologues of the rhynchonelloid spires. But what she has taken as crescentic trocholophes are actually, as can be seen from the arrangement of the filaments in her text-fig. 4a-b, zygolophes of individuals about 4 mm. long.

The difference then between the spirolophe and the plectolophe is simply dependent on the attitude of the first formed coil relative to the rest of the spire for either half of the lophophore. In the terebratuloids, the left side arm is essentially the first coil, narrowly compressed in the ventro-dorsal plane, which is added to from a plano-spire lying out-

side its periphery and coiling in a clockwise direction (text-fig. 2*a, b*). In rhynchonelloids, the first coil of the left half of the lophophore is not compressed so that the helicoidal spire lies within it, and coiling takes place in an anticlockwise direction (text-Fig. 2*c, d*). These changes in growth directions must be related to the disposition of the generative zones, which are medianly paired in the schizolophous stage. For in the plectolophes they persist in the median plane, and coiling can only begin with movement away from the diaphragm, that is with a clockwise revolution of the left zone and an anticlockwise one of the the right. In the rhynchonelloid spirolophes the generative zones migrate away



TEXT-FIG. 2. Stylized ventral and lateral views of a terebratuloid plectolophe (*a, b*) and a rhynchonelloid spirolophe (*c, d*) to show the positions of the original trocholophes, the primary coils, and the generative zones.

from the median plane as the apices of two ever-increasing spires directed dorsally or antero-dorsally and coiled anticlockwise on the left and clockwise on the right. The persistence of the generative zones on the median plane or migration laterally away from it now become matters of some importance, and, since the first condition is exclusive to the loop-bearing terebratuloids while the second is characteristic of those brachiopods equipped with nothing more than the crura, physical constraint by the brachidial skeleton may well account for the difference. Thus the terebratuloid schizolophe is either contained laterally by a pair of calcareous ribbons growing from the crural ends (in the terebratulaceids and the majority of the terebratellaceids) or is intimately associated with the median septum which separates the generative zones (in all terebratellaceids).

The constraint exercised by the early growth of a loop and/or a median septum with divergent plates (e.g. *Kraussina*) is such that one of only four modifications can take place. Where the enlargement of the loop is as fast as the proliferation of the filaments and the lophophore, the structure retains the simplicity of the early stages in development. This probably occurred in early terebratuloids like *Rensselandia* (see Williams 1956, text-fig. 5 (10)) and is also characteristic of certain stocks like *Argyrotheca*.

In the second group, growth of the loop is slower than the total growth of the lophophore, but more or less keeps pace with the enlargement of a pair of side arms. The dis-

tortion of the subcircular outline of the schizolophe by the development of a pair of anteriorly directed bulges, which later become side arms, is to be expected when proliferation from medianly disposed generative zones is very much greater than postero-lateral migration of the lophophore. As a support to the side arms, the original simple loop of the majority of the terebratulaceids is refashioned by complex processes of resorption and secretion, and is greatly enlarged anteriorly. Nevertheless, the production of a lophophore at the two median tips is ultimately so much faster than its incorporation into the lengthening side arms that the growth zones push themselves away from the diaphragm and begin to coil antero-ventrally, and so give rise to the terebratulaceid plectolophe.

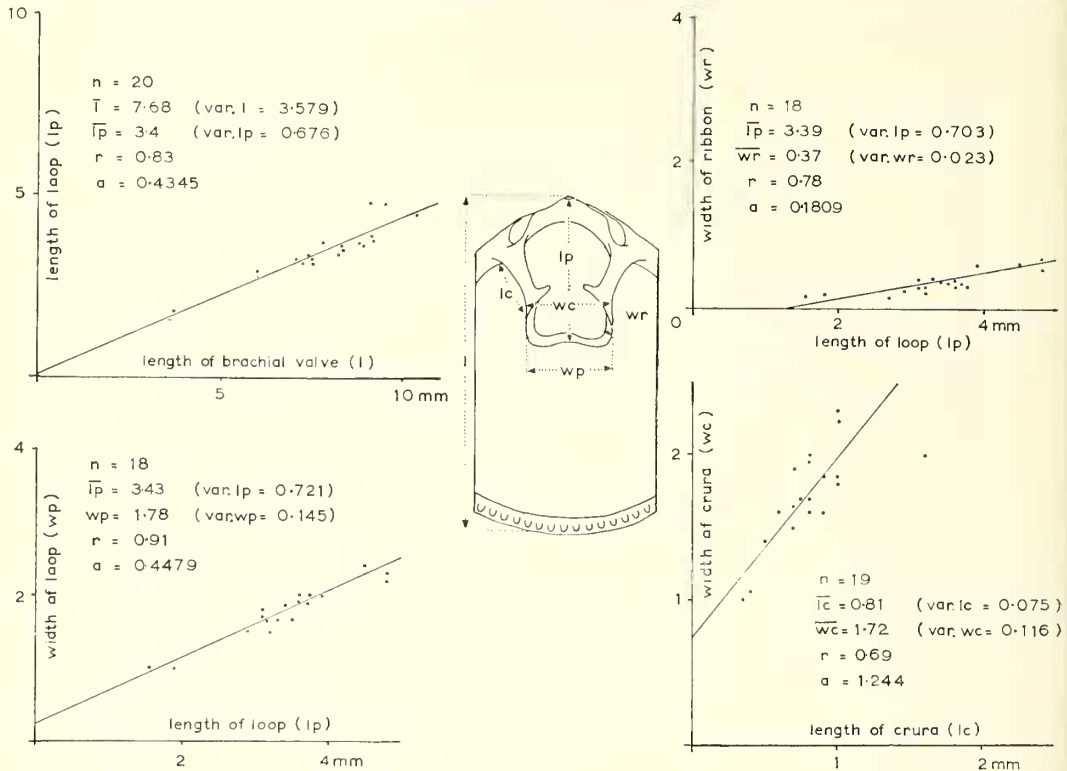
The third group includes those forms in which the growth of the skeletal supports to the lophophore is so much slower than the expansion of that organ that there is little morphological similarity between the calcareous and fleshy parts of the apparatus. The short terebratulaceid loop supports a plectolophous lophophore in such a way that only the posterior semicircle of the lophophore and the junctions between the side arms and the median coils rest upon it. Presumably proliferation at the growing tips is so much greater than the enlargement of the loop that the side arms are squeezed out of the confining circle antero-laterally, as a pair of closely united loops, and the generative zones themselves move away from the diaphragm to describe a pair of contiguous plano-spires. In the kraussinids, the growth of divergent lamellae from the median septum, to which the adjacent generative zones are attached, provide a similar restriction. The consequences are well seen in *Pumilus antiquatus* Atkins, because in this species the schizolophe of the adult shows an exaggerated sweep of the antero-lateral parts of the lophophore, which is precursory to the development of the ptycholophe or the plectolophe of *Kraussina*.

The fourth group is visualized as including those forms in which the expansion of the loop is slower than the growth of the lophophore, but in which the excess length of the latter is supported by apophyses growing out from a relatively short loop. Imagine, for example, a pair of single ribbons growing out of the antero-lateral part of the *Terebratulina* loop to give support to the side arms, which are in any case so closely united as to be served by a single brachial canal. No living brachiopods display this pattern, but a Devonian centronellaceid, *Cimcinella* (Schmidt 1946), does, and it is believed that the calcareous spires of the spiriferoid brachiopods should be interpreted in this way (Williams 1956, pp. 269-71). These fossil stocks are more appropriately discussed below in the section concerned with the origin of the loop.

In the preceding discussion reference has been made to the unequal growth rates of the lophophore and its skeletal supports, with the implication that the two structures are independently controlled in spite of a good deal of interdependent adjustment during development. The origin of the internal calcareous parts of brachiopods, whether they are crura, spires, or loops has aroused comment for over a century. Hancock (1859, p. 831) believed that the inner epithelium (i.e. his 'lamina') was responsible for their secretion. Morse (1871) asserted that the terebratulid loop was formed by amalgamation of spicules. In 1956 Williams (p. 266) said that all such growths were secreted by outer epithelium in exactly the same way as the secondary layer of the shell. Serial sections of *Terebratulina*, *Terebratella*, and *Terebratalia* show that their apparatuses, continuous as they are with either the crura or the median septum, are contained in



sheath-like extensions of the outer epithelium, which is responsible for the secretion of those two structures. What happens when two calcareous pieces become united can be safely inferred from a study of the development of the *Terebratulina* loop in sectioned specimens. The convergence of the lamellae descending from the crura towards the median plane brings the epithelial tips of the descending branches together. Secretion continues until both epithelial layers, one across each tip, are destroyed, but peripherally



TEXT-FIG. 3. Some biometrical attributes of the growth of the *Terebratulina* brachial apparatus.

they fuse to form one continuous sheath. This mode of secretion has been restated and enlarged upon because Hyman (1959, p. 549) repudiates the interpretation and favours the deposition of the loop by connective tissue presumably in the manner suggested by Morse. Her rejection of epithelial secretion appears to be founded on the failure of the author responsible for this idea (Williams 1956, not Elliott 1956 as given by her) 'to explain how this epidermis could get inside the lophophore'. Invagination of one epithelial layer so that it grows in association with connective tissue surrounded by another layer is, however, a common feature of animal growth, and its role in the development of the loop may be confirmed in suitably prepared sections.

The construction of skeletal supports to the lophophore by invaginations of the outer epithelium is demonstrably a complex interplay between secretion and resorption of fibrous calcite, which can be appreciated by considering some biometrical aspects of loop variation in a small sample of *Terebratulina* (text-fig. 3). The crura and the proximal

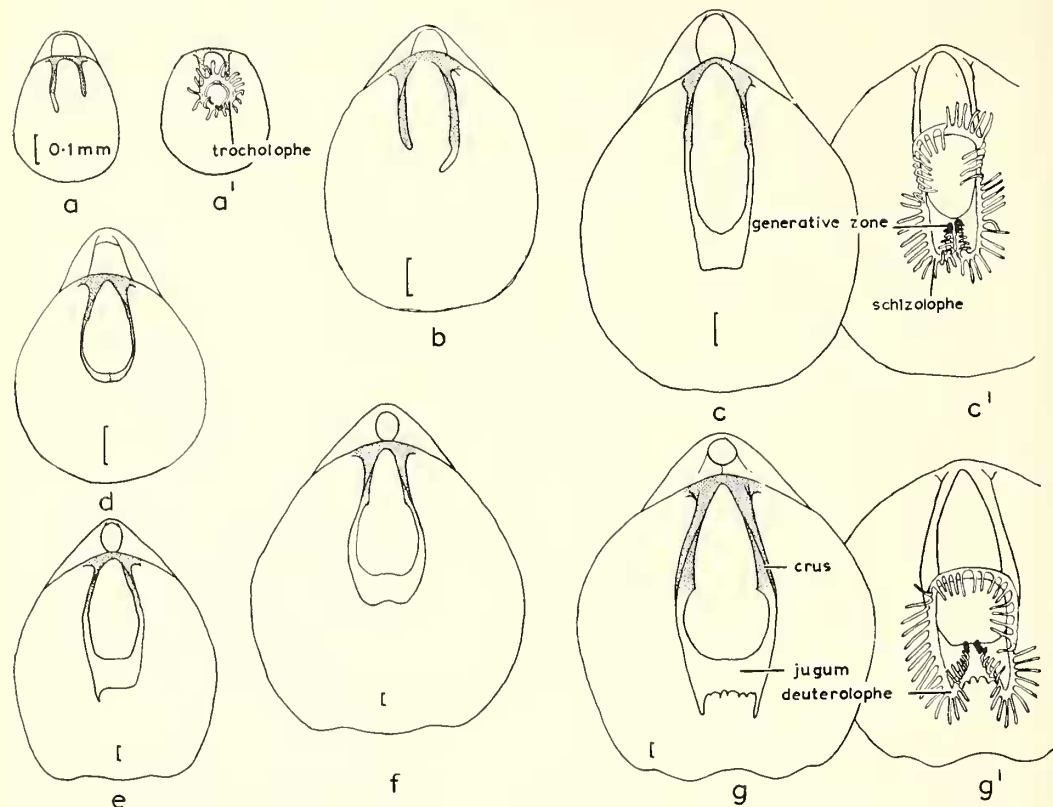
parts of the descending branches must be secreted when the lophophore is trocholophous and before the brachial valve has attained a length of 1 mm., because an early plectolophe supported by a nearly completed loop occurs in valves 2 mm. long. Fusion of the descending branches is usually effected before the valves are 4 mm. long, but one specimen of that size has been sectioned in which the calcareous ribbons were still discrete. Thereafter, the loop increases steadily, laterally and also anteriorly, to maintain a length about half that of the valve. The calcareous ribbon also increases in width, but not at a rate which could account for the overall enlargement of the loop without a concomitant resorption taking place along its inner edge. The same sort of functional differentiation must also obtain in the epithelial sheath to the crura. These processes arise from the antero-lateral parts of the inner surfaces of the socket ridges. They are convergent towards the median plane, so that their growth in length should result in a narrowing of the distance between their tips. Instead, there is a widening of the gap, and this can only come about if the crural bases 'move' apart in antero-lateral directions away from the umbonal region. Such modification must again be due to resorption of the inner surfaces of the crura, and simultaneous secretion on the outer surfaces by the surrounding epithelium. Among the terebratulaceids this method of fashioning and enlarging the supports to the lophophore goes on with even more profound results. It involves, among other things, the degeneration of a septum and the development of long loops, ultimately a continuous calcareous ribbon disposed as a pair of U-shaped lateral lobes, by the fusion of two distinct elements—the descending branches and the hood which first develops from the septum (Elliott 1953). These developments clearly involve both deposition and resorption over the entire surface of the supports, and there is no doubt that, although the growth of certain structural parts, like the descending branches, may be indicative of localized accelerated secretion, the entire epithelial surfaces must be capable of proliferation in a manner quite unlike that of the origin of the lophophore. Consequently, any conformity existing between the calcareous and fleshy parts of the feeding apparatus is really a compromise between two entirely different processes of growth.

#### THE LOOPS OF FOSSIL BRACHIOPODS

Whatever the differences between the attitude of the fully grown lophophore and the disposition of its calcareous support (and, as in the terebratulaceids, the differences may be profound), two generalizations can be safely assumed for all fossil brachiopods, including extinct groups. The first is that the crura always lay within the body chamber and gave support to the postero-median strip of the lophophore which contained the mouth. This is as true for living rhynchonelloids as it is for Recent terebratuloids, and there is no justification for a different interpretation for comparable processes in other articulate brachiopods. The second is that the lophophore of any young specimen, less than 1 mm. in length, was either a simple trocholophe or a very early schizolophe with the generative zones located antero-medianly. This is so for *Macandrevia cranium*, *Terebratella inconspicua*, *Pumilus antiquus*, *Platidia davidsoni*, *Terebratulina capnt-serpentis* (Linnaeus), *Hemithyris psittacea* (Gmelin), and *Tegulorhynchia nigricans* (J. de C. Sowerby), and it follows that the growth of a pair of descending branches from the crural ends, and their antero-median fusion to form a loop at this stage of development, represents the secretion of a peripheral support to a subcircular lophophore. Both assumptions are important, because they provide a means of assessing the nature and

disposition of the lophophore in wholly extinct groups, and, since the crura and the loop were developed in the spiriferoid brachiopods long before the terebratuloids first appeared, it is now appropriate to consider the origin of these supports.

The earliest known spiriferoid is the Ordovician stock *Protozyga* Hall & Clarke. Cooper (1956, p. 681) has described a species, *P. microscopica*, from the Elway formation of

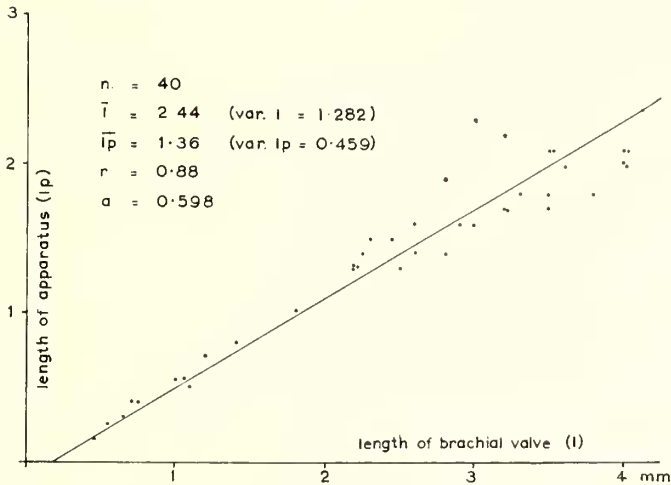


TEXT-FIG. 4. The growth of the brachial apparatus of *Protozyga elongata* Cooper with reconstructions of the trocholophe (*a'*) and the schizolophe (*c'*, *g'*).

Tennessee and a number of others are known from the post-Chazyan of America and the Caradocian of Scotland. A good sample of one of these, *P. elongata* Cooper, was collected by one of us from the Bromide beds exposed one mile west of Dolese Brothers' Crusher, Bromide, Johnson Co., Oklahoma. The majority of specimens, of all sizes, are filled with clear calcite, so that by grinding away the exteriors of both valves it is possible to see the arrangement of the internal skeleton, and thereby infer development during growth. The earliest growth stage examined is represented by shells with brachial valves slightly less than 0.5 mm. long, in which a pair of delicate, slightly divergent prongs extend anteriorly from the hinge line for slightly less than one-third the length of the valve. In the specimen figured (text-fig. 4*a*, *a'*) the left prong is longer than the right, but this extra part of the ribbon converges towards the median plane, and it is feasible to suppose that both prongs gave support to the posterior arc of the trocholophe, in the



manner of crura, and that the additional strip on the left represents the beginnings of a descending branch. A similar asymmetrical growth involving the right prong is seen in another valve 0.75 mm. long (text-fig. 4*b*). But more often than not, both descending branches developed and fused antero-medially before the valve attained a length of 1 mm., and this is known to have occurred when the valve was no more than 0.7 mm. long (text-fig. 4*d*), although suggestions of a suture along the median plane of contact between the two branches probably implies that fusion had not then been completed. By this stage of growth, the loop was already orientated towards the pedicle valve in an



TEXT-FIG. 5. A correlation between the growth of the brachial apparatuses and the growth of brachial valves of *Protozyga elongata* Cooper.

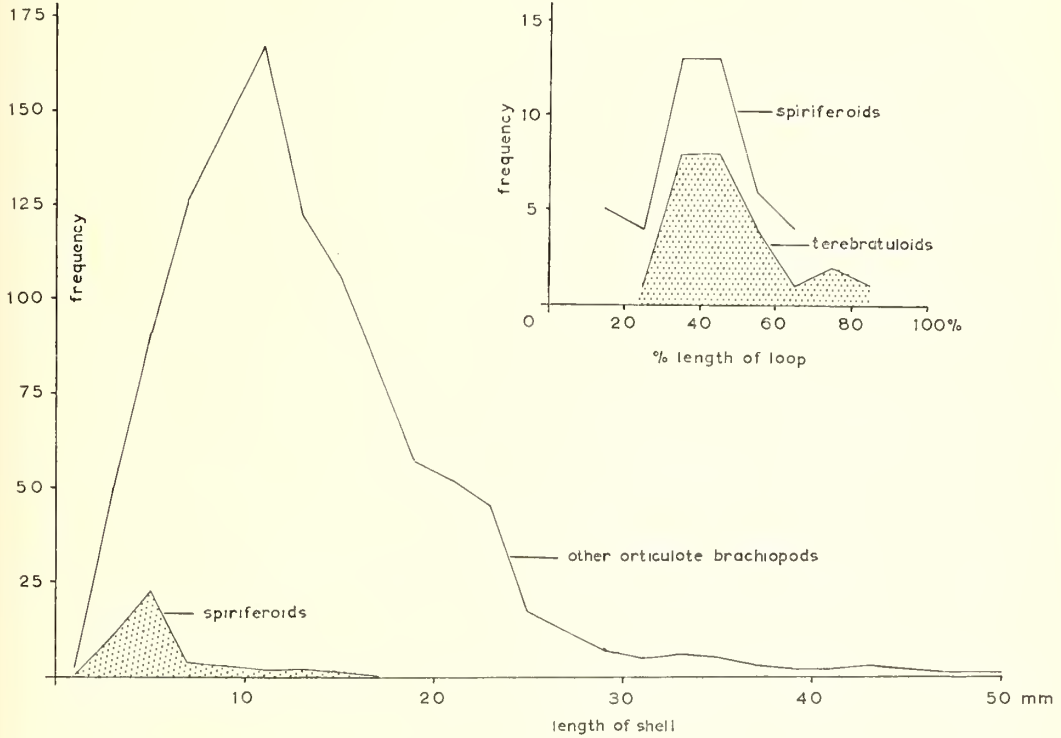
attitude characteristic of adult shells, due to the antero-ventral expansion of the descending branches, which met obliquely so that the zone of fusion tended to form a crest to the transverse part of the loop. It is inconceivable, in shells as small as this, that the loop supported any lophophore more complicated than either a trocholophe or an early schizolophe (text-fig. 4*c*, *c'*), and it is therefore realistic to assume that the paired generative zones were located about or on the median line of fusion. In subsequent development the loop expanded anteriorly at about half the rate of shell elongation, although there was considerable variation (text-fig. 5). It also expanded laterally and, although the calcareous ribbon increased in width, especially along the transverse part of the loop, the enlargement must have involved resorption of the inner margins as well as secretion along the outer one by the outer epithelial sheath. Even in the largest adult shells, which are rarely more than 4 mm. long, the loop was the sole brachial support, but it tended to become truncated anteriorly (text-fig. 4*e*, *f*) and, exceptionally, from the antero-lateral corners thus formed, a pair of short apophyses grew in an anterior direction (text-fig. 4*g*, *g'*). These prolongations are homologous with ones which grew into a pair of arcs or even coils, disposed in a ventro-dorsal plane on either side of the loop, in other species of *Protozyga* (Cooper 1956, p. 675), and are therefore the beginnings of the calcareous

spires of the early spiriferoids. Their appearance may therefore be used to identify the transverse part of the loop as the homologue of the spiriferoid jugum.

Having recognized the principal elements of the spiriferoid endo-skeleton as they emerge during the development of *Protozyga*, it is now possible to infer the disposition of the lophophore. The most significant aspect of *P. elongata* is that it is a loop-bearing stock, and only potentially a spiriferoid in the more orthodox sense. Indeed, were it not for its stratigraphical context, and, less importantly, its impunctate shell, it would be more appropriately classified as a terebratuloid, and, in the circumstances, no one would doubt the persistence of the paired generative zones, responsible for the growth of the lophophore in the median plane of the jugum, throughout the development of living shells. Even the growth of a pair of curved calcareous ribbons from the antero-lateral corners of the loop would not cause much concern, because the antero-lateral lobation of the lophophore to fit around the periphery of each outgrowth would be strictly homologous with the side arms of *Terebratulina* if they were each stiffened by a calcareous ribbon arising from the loop. It was for this reason that the term of *deuterolophe* was used by Williams (1956, p. 270) to define a lophophore which extended laterally as a pair of narrowly compressed loops, each supported by a single calcareous ribbon arising from the junction of the jugum with the descending branches of spiriferoid brachiopods (text-fig. 4g'). The fact that in spiriferoids the side ribbons continued to grow into coils arranged in planar or helicoidal spires does not necessitate any important modification of the basic lophophore arrangement, like the migration of the generative zones away from the median plane so as to coincide with the epithelial tips of the calcareous spires. On the contrary, there is sound evidence to suggest that such a migration did not occur. The jugum of athyraceids is prolonged posteriorly as a calcareous process. This jugal stem bifurcates in a number of stocks, e.g. *Athyris*, to form a pair of arcs (the accessory lamellae) lateral to the first coils of the deuterolophe, and, in certain unrelated athyraceids like the Devonian *Kayseria* and the Triassic *Diplospirella*, the accessory lamellae continued to grow into a pair of spires coextensive with those of the deuterolophe (Williams 1956, p. 270, fig. 5 (9)). If the generative zones moved away from the jugum at all, it is much more likely that they did so posteriorly along the jugal stem and then laterally in association with the accessory spires, and it is these spires which must be homologized with the rhynchonelloid spirolophe, not those giving support to the deuterolophe, which is really equivalent to the side arms of the terebratuloid.

The earliest spirebearer, *Protozyga*, has thus provided some interesting information on the growth of the loop, which is supplementary to that given by Beecher and Clarke (1889) in their classical study of the development of the deuterolophous spires of *Zygospira* subsequent to the formation of the loop. Only a few other growth series have been described, but it is probable that the loop is basic to the growth of all calcareous spires, and its origin may be better understood by comparing the Ordovician spiriferoids with their other articulate contemporaries. It is known that those early spiriferoids were not alone in possessing crura, because Ordovician rhynchonelloids, syntrophiaceids, and some orthoids were equipped with similarly proportioned outgrowths from the hinge-line, which presumably also give support to the posterior part of the lophophore. Development of descending branches, however, was unique to the spiriferoids, and their appearance in very young growth stages of *P. elongata* emphasizes the coenogenetic nature of the loop.

This was effectively combined with another important attribute. Sexual maturity is attained quite early on in the life history of living brachiopods. Morse (1873, p. 36) found eggs in individuals of *Terebratulina septentrionalis* no more than 5 mm. long, which is about one-quarter the size of mature adults, although even at that size the lophophore is likely to be an early plectolophe. Atkins (1958, p. 567) reports sexual



TEXT-FIG. 6. Frequency distributions of the longest pedicle valves recorded in the type descriptions of forty-six Ordovician spiriferoid species and 1,113 other contemporary species of articulate brachiopods. In the smaller graph: frequency distributions of the length of the loops (measured from the dorsal umbones to the posterior edges of the transverse bands and juga) relative to the length of the brachial valves of twenty-five terebratuloid and forty-five spiriferoid Silurian and Devonian genera.

maturity in specimens of *Pumilus antiquatus* which were slightly more than one-third the size of adults, when the lophophore was in the early schizolophous stage of development. The sexual precocity of *P. antiquatus* relative to the lophophore is all the more noticeable, because senile specimens are not more than 5 mm. long, and this size discrepancy between, for example, *Pumilus* and *Terebratulina*, is also seen when early spiriferoids are compared with other brachiopods of the same age.

Text-fig. 6 shows the frequency distribution of the lengths of adult shells (derived from measurements of type specimens) of forty-six Ordovician species, distributed among nine spiriferoid genera, and 1,113 other species, belonging to 185 contemporary non-spiriferoid articulate genera. Both distributions are similar in being positively skewed, so that only a minority of stocks attain a relatively large size, but the modal length of adult



spiriferoids at 4–5 mm. is less than one-half the modal length of the remainder. The discrepancy is even more striking in the earliest known spiriferoid stocks like *P. elongata*, adults of which rarely exceed 3 mm., and if sexual maturity occurred at the same relative stage of growth in that species as it does in living brachiopods, then individuals of *P. elongata* were functional adults about the time when fusion of the descending branches occurred. *Protozyga* then could well have been derived neotenously from some existing group, preferably impunctate and rostrate in the manner of contemporary rhynchonelloids. Moreover, the endowment of a new coenogenetic character like the loop with an unspecialized juvenile anatomy, including a trocholophous lophophore, meant that the prospects for full exploitation of this novelty during subsequent radiation were quite good.

The origin of the terebratuloids can only be seriously considered in the light of what has already been stated. The oldest representatives of this suborder are the centronellaceids, *Podella*, *Mutationella*, and *Brachyzyga* (Kozłowski 1929, pp. 232–45) from the Upper Silurian of Poland. The development of the loops characteristic of these three genera is unknown, and, of all other centronellaceids, only the young stages of the Devonian *Cranaena* (Stehli 1956, p. 191) and the Permo-Carboniferous *Dielasma* (Beecher 1897, p. 110) have been described. It is, however, generally and safely assumed that all adult centronellaceid loops were derived, by processes of resorption and differential growth, from a simple lanceolate apparatus, known as the centronelliform loop, which is common to the early stages of both *Cranaena* and *Dielasma*, and which persisted, with little or no modification, as the adult loop in a number of Devonian stocks. The centronelliform loop is identical with the one found in young *Zygospira* shells (Beecher 1897, p. 111) and is strictly homologous with the *Protozyga* one. It must, therefore, have given support to a trocholophe or an early schizolophe, with the generative zones disposed contiguously about a median lamella whenever that structure developed. Subsequent growth is not difficult to envisage. In adult *Rensselandia*, *Centronella*, and the majority of *Mutationella*, &c., the fundamental pattern was retained, simply by resorption along the inner margin of the loop and secretion along the outer edge, so that a greatly enlarged trocholophe probably served as the feeding organ of adult shells. A more important and successful modification included resorption of the antero-median part of the loop and the refashioning of the corroded connexion into a transverse, posteriorly curved band making acute angles with the descending branches. Without further modification, except enlargement, this structure constitutes the short loop of *Cranaena* and *Dielasma*, and is also anticipated in a minority of adult *Mutationella* (Kozłowski 1929, p. 241). It is also like the terebratulaceid loop and, although the connecting band in this case results from the convergence of the descending branches and not from the modification of a pre-existing centronelliform loop, the independent expansion of the lophophore from a pair of median generative zones in *Cranaena* and *Dielasma* could well have given rise to a pair of fleshy appendages hanging free from the antero-lateral corners of the loops, in the manner of the terebratulaceid side arms.

A recognizable plectolophe must certainly have existed in *Cryptonella* (Cloud 1942, pl. 22, figs. 16–20), because in this stock differential antero-lateral growth of the centronelliform loop resulted in the development of an apparatus duplicating the arrangement of the terebratellaceid long loop. It must also have been present in *Cimcinella* (Schmidt 1946), the loop of which is essentially like that of *Cryptonella*, except that the descending and ascending branches are ankylosed to form a pair of ribbons extending

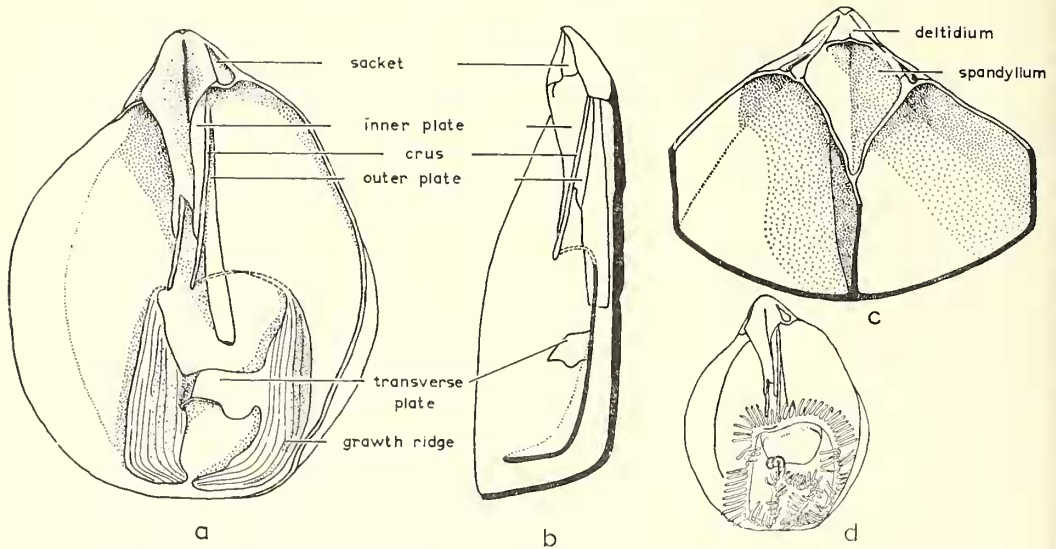
anteriorly from the junctions of the transverse band with the descending branches. *Cimcinella* is remarkable because its lophophore support is morphologically comparable with the late growth stages of *Protozyga* and early post-centronelliform stages of *Zygospira*, where the calcareous ribbons, which gave support to the deuterolophe, had not quite completed half coils of the first pair of spires.

The transverse connecting bands of these early terebratuloids clearly arose in exactly the same way as the jugum of the spiriferoids, and there can be little doubt that those portions of the terebratuloid and spiriferoid apparatuses, lying posteriorly to the band and the jugum respectively, are identical in origin, and presumably give support to similarly disposed lophophores. Even in adult shells the 'loops' thus defined by the transverse bands and juga are closely comparable in proportions. Text-fig. 6 shows the length of these loops, measured from the dorsal umbo to the inner edges of the transverse bands and the juga, relative to the lengths of the brachial valves of twenty-five terebratuloid and forty-five spiriferoid genera of Silurian and Devonian age. In both suborders it is seen that the modal length of the loops was about two-fifths that of the brachial valve. The terebratuloid loop, then, was most feasibly derived from the spiriferoid brachial skeleton simply by a suppression of the growth of the calcareous spires. Furthermore, since the development of the spires was preceded by the secretion of a loop, it may be assumed that the earliest terebratuloids were small, generalized shells of pre-Ludlow age, distinguishable from the juveniles of contemporary, punctate spiriferoids, from which group they were probably neotenously derived, mainly in physiological differences responsible for the early sexual maturity of the former.

Two Devonian loop-bearing genera which do not fit into the scheme of derivation outlined above are *Enantiosphen* Whidborne and *Tropidoleptus* Hall. A number of studies have been made of these two stocks, notably by Holzapfel (1912), Leidhold (1928), and Torley (1934) who concluded, with varying degrees of conviction, that *Enantiosphen* is a pentameraceid, and by Hall and Clarke (1893) and Schuchert and Cooper (1932) who respectively assigned *Tropidoleptus* to the *Terebratellacea* and the *Dalmanellacea*. The descriptions given by these authors were based on dissected specimens and, although the preparations were adequate enough to reveal the general morphology of the loops, no satisfactory illustration of the interiors and no detailed account of the shell structure have yet been given. To remedy this deficiency, a few specimens of both genera were serially sectioned, to obtain cellulose impressions of shell surfaces which had been differentially etched to reveal the details of shell growth. In addition, large-scale models of the shells were reconstructed by fusing together, with a hot needle, successive layers of 'tenastyle' wax, each of which had been first cut into an outline coincident with that on an enlarged photograph of the impressions on each cellulose peel.

*Enantiosphen* is an impunctate, rostrate stock with a smooth, or faintly and sporadically costate, exterior and unusually disposed valves. The transversely oval outline, and gently and subequally biconvex profile of some species (like *E. torleyi* Holzapfel) are fairly orthodox, but postero-medianly, the edges of the valves are sharply deflected inwards to define a pair of false 'interareas', each lanceolate in outline and situated on either side of the umbones. In *E. vicaryi* (Davidson) this deflexion affects the entire shell, so that wide margins of both valves are sharply geniculated towards the commissural plane to give the shell a trigonal, wedge-like aspect in profile and outline, and this, as will be seen, is accompanied by a similar ventral deflexion of the loop.

The morphology of the pedicle valve is typically pentameraceid (text-fig. 7c). The incurved umbo contains a narrowly triangular delthyrium, partly receiving the ventrally projected dorsal umbo, and covered posteriorly by a slightly convex deltidium. The deltidium is seen in section (text-fig. 8a) to be buttressed by secondary shell substances, which must have been secreted by outer epithelial extensions encroaching ventro-anteriorly on to the inner spondylial surface, and, since these extensions could only have existed ventral of the pediculate-outer epithelial junction (Williams 1956, p. 257), the pedicle itself must have atrophied in adult shells at least. The spondylium (text-fig. 8b, c) is



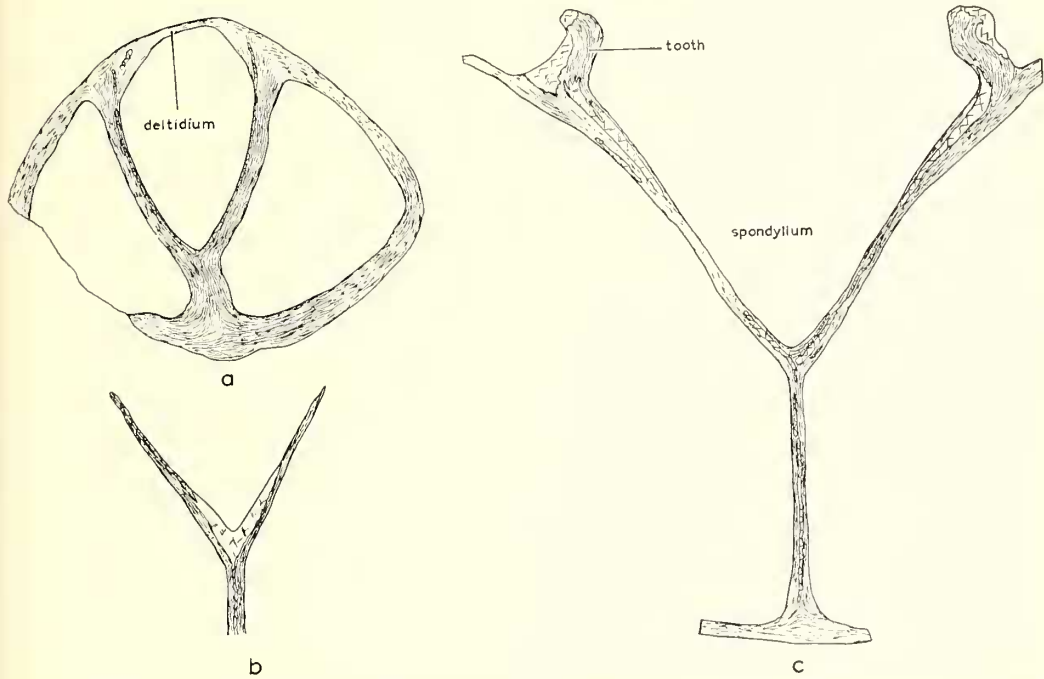
TEXT-FIG. 7. The internal morphology of the brachial valve, in ventral (a) and lateral (b) views, and of the pedicle valve, in antero-dorsal view (c), of *Enantiosphen vicaryi* (Davidson): together with a stylized reconstruction of the lophophore (d).

of a kind which is usually referred to as 'duplex', in the sense that the supporting septum is made up of secondary fibrous calcite, incompletely divided into two partitions by a thin median prismatic layer. Prismatic calcite also occurs on and within the spondylium itself, and again along the outer edges of the teeth, largely supported by the spondylial walls, as a series of wedges and lenses (text-fig. 8c). These are seen to pass laterally into fibrous calcite and, since the definition of each fibre was originally due to its being contained within a cytoplasmic sheath-like extension of an outer epithelial cell, it must be concluded that the prismatic patches were extra-cellular secretions by the outer epithelium (Williams 1956, p. 250). The primary outer shell layer is also secreted in a similar way, and St. Joseph (1938, p. 244) believed that the median prismatic layer, which is commonly found embedded in the fibrous calcite of the spondylial septum of pentameroids as well as *Enantiosphen*, was deposited by the mantle edge. This is impossible, because it implies that the septum originated at the antero-median edge of the pedicle valve, whereas it arises well within the valve margin. Also, the presence of prismatic calcite in the median plane of the septum is not in our view indicative of any difference in the origin of the septal support to the spondylium duplex as compared with that of the spondylium



simplex, which is purported to consist of fibrous calcite alone. The terebratuloid *Amphigenia* Hall is also equipped with a spondylium, but this structure is quite unlike the pentameroid ones, for it is buttressed by a pair of mystrochial plates, and has been shown (Boucot 1959, p. 737) to have developed from discrete dental lamellae as in *Rensselaeria* Hall.

The cardinalia of the brachial valve of *Enantiosphen* are also pentameraceid in arrangement (text-fig. 7a, b). The rod-like crura, which extend anteriorly for about one-half the

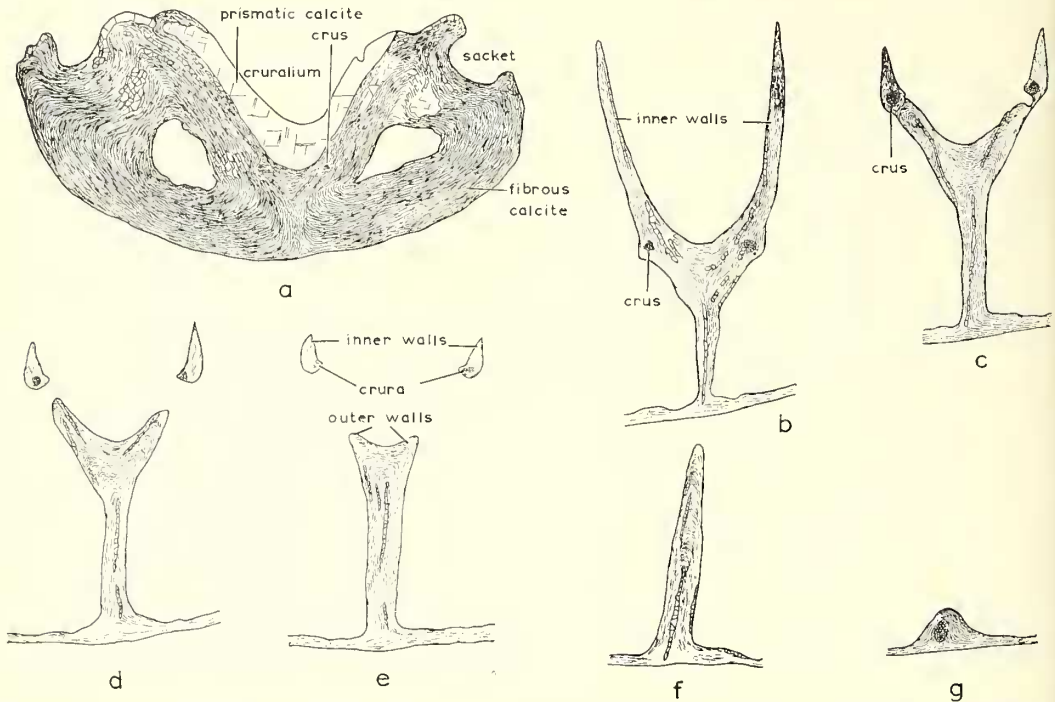


TEXT-FIG. 8. Three sections showing the structure of the spondylium in the pedicle valve of *Enantiosphen vicaryi* (Davidson)

length of the valve, can be traced from the umbo. In this region they are deeply embedded in thick deposits of secondary, fibrous and prismatic calcite, which make up the massive posterior part of the cruralium, but anteriorly their relationship with other elements of the cardinalia are easily seen (text-fig. 9a-e). It is evident that they are intimately associated with the slightly convergent blade-like inner plates, which are continuous ventrolaterally with the socket ridges, and which form the lateral walls of the cruralium. The essential unity of the inner plates and crura is illustrated by the manner in which they both become discrete from the outer plates at about one-third the length of the valve anterior of the umbo (text-fig. 9d, e). The outer plates, which are really a pair of ridges diverging from a stout septum, form the basal part of the cruralium. They retain their identity for a short distance anterior of their separation from the crura and the more ventrally placed inner plates, but ultimately they, and then the median septum, are no longer found (text-fig. 9f, g).

Just anterior to the tips of the crura, the posterior ends of the loop are found at some

distance dorsal of the extrapolated positions of the crura. The actual connexions between the loop and the crural tips have not been identified, but the gap between the tips and the first traces of the loop is not more than a millimetre or so thick, and it seems safe to assume that the connexions actually swept dorsally away from the crural points, more or less in the same plane as the sectioning in the style illustrated by Leidhold (1928, pl. 5, fig. 3). The brachial apparatus is unique, for it consists essentially of two broad



TEXT-FIG. 9. Seven sections showing the structure of the cardinalia and the cruralium and its supporting median septum in the brachial valve of *Enantiosphen vicaryi* (Davidson).

plates, composed of fibrous calcite and essentially suboval in outline, but curving along the lateral edges towards the ventral valve and crenulated in transverse section by a series of ridges running more or less concentric with the lateral edges of the blades. Posteriorly, the blades narrow rapidly to form ribbon-like connexions with the crural points. Anteriorly, they taper more gradually into blunt ends which are either in the same plane, as the rest of the blades, for example, in the gently biconvex *E. torleyi* (Torley 1934, p. 97, fig. 28), or deflected sharply towards the pedicle valve, as in the bigeniculate *E. vicaryi*. The two blades are united by a variably developed transverse plate which rises to a sharp ridge ventro-medially. The transverse plate is also composed of fibrous calcite and appears to be continuous with the lateral blades, but its position relative to them seems to vary considerably, so that in some specimens it connects the postero-medial edges of the lateral blades while in others it may occur between the anterior ends. Leidhold (1928, p. 58) maintained that the apparatus was supported by the anterior part of the dorsal median septum. This is not so in the specimen sectioned by us, and Torley makes

no mention of such an arrangement in the shells he examined, which suggests that those described by Leidhold had been imperfectly prepared, and indeed, in one specimen figured by him (pl. 5, fig. 2), the arrangement he suggests would have been impossible.

The lack of young specimens precludes any precise assessment of the role of the *Enantiosphen* apparatus in its support of the lophophore, but a number of adult features give some guide to possible relationships. The blades, consisting as they do of fibrous calcite, were secreted by a bilobate envelope of outer epithelium continuous with those extensions from the floor of the brachial valve which ensheath the crura. The ridges, which are roughly aligned with the lateral edges of the blades, probably represent pauses in an erratic antero-lateral expansion of an outer epithelial cover to what was initially a subcircular ribbon of calcite suspended from immature crura. Resorption must have taken place along the postero-median edges of the epithelial envelope to adjust the connexions of the apparatus to the divergent forward growth of the crura. But it was so much slower than the secretion along the antero-lateral margins that a pair of blades developed in adult stages of growth. Variation in the rates of resorption and secretion was probably also responsible for the range in width and position of the transverse band from one individual to another. Neither the blades nor the transverse bands thicken consistently in a postero-median direction, which suggests that only the outer edge of the epithelial cover was engaged in the secretion of fibrous calcite in a manner similar to the growth of the campagiform loop of certain terebratellaceids (for example *Fallax dalliniformis* Atkins 1960). In these circumstances it is reasonable to assume that the lophophore was intimately associated with the secretory zone of the outer epithelium and accordingly was essentially schizolophous in disposition (text-fig. 7d). It is not possible to decide whether the median generative zones existed free of the crest along the transverse plate as a pair of spires coiled in a plane normal to the commissure. The proximity of the plate to the floor of the valve, together with its variable position, suggests that if coiling had taken place it must have been towards the ventral valve.

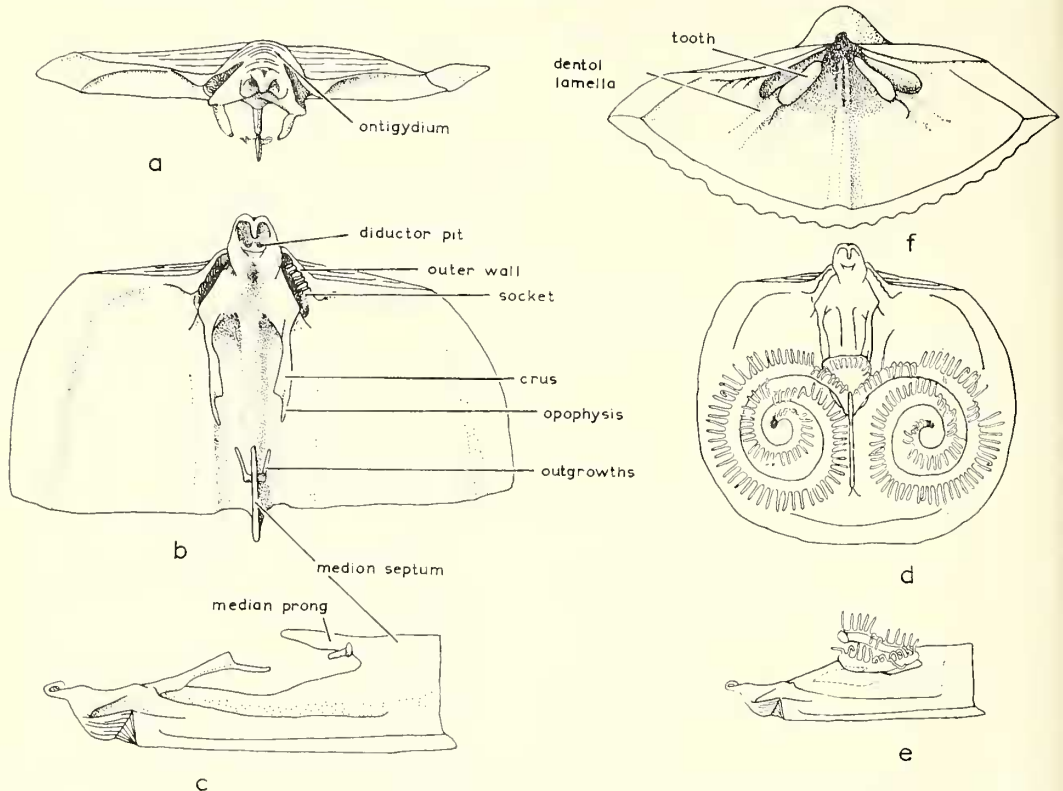
In summary, it may be said that *Enantiosphen* is undoubtedly a pentameraceid brachiopod which is unique in that adult shells were equipped with a bilobate brachial apparatus. The apparatus probably developed by differential growth and resorption from a simple subcircular loop, presumably surrounding a juvenile trocholophe, and is most reasonably interpreted as having supported a schizolophous-like lophophore. The structure is not closely comparable with the loops of contemporary centronellaceids, except, of course, that its development likewise imposed certain restrictions on the attitude to be adopted by the adult lophophore. Accordingly, the inferred disposition of the lophophore was not necessarily typical of other pentameraceids, the crura of which were more likely to have supported spirolophes like those found in recent rhynchonelloids.

*Tropidoleptus carinatus* (Conrad) is a costate brachiopod, subquadrate in outline with a concave and medianly sulcate brachial valve, and a convex pedicle valve which is narrowly folded medianly. In other external features, notably the wide hinge-line and the well-developed, orthocline, ventral interarea and the shorter, anacline, dorsal one, and also in the coarsely endopunctate structure of the shell, the genus is undoubtedly a dalmanellaceid.

The interior of the pedicle valve is also organized in a dalmanellaceid manner (text-fig. 10f). The delthyrium is not restricted by any deltidial outgrowth, and, during the life of the animal, was filled by the cardinal process so completely that no functional pedicle



could have existed in adult shells at least. The teeth are massive, elongated and ridge-like, and exhibit the extremely rare disposition of being completely separated from the hinge-line by a pair of deep, oblique grooves which accommodate the outer walls to the dorsal sockets. They lie in the same plane as, and are supported by, a pair of widely divergent dental lamellae which extend beyond the umbonal cavity only as subdued

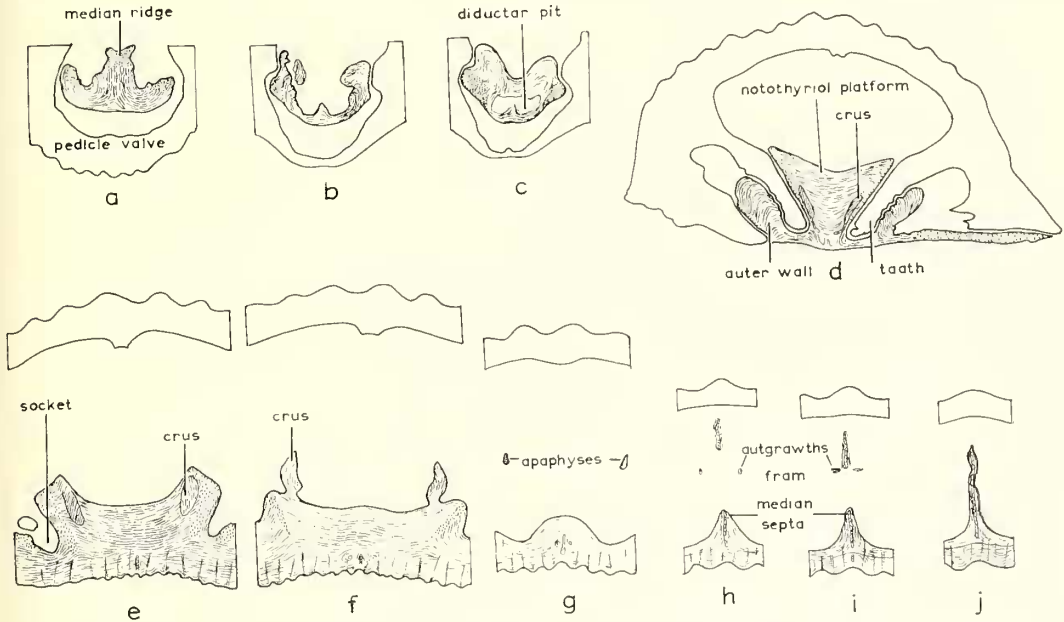


TEXT-FIG. 10. The internal morphology of the brachial valve, in posterior (a), ventral (b), and lateral (c) views, and of the pedicle valve, in antero-dorsal view (f), of *Tropidoleptus carinatus* (Conrad): together with stylized reconstructions of the lophophore in ventral (d) and lateral (e) views.

traces. The inner surfaces of both the teeth and lamellae are smooth and fit snugly against the undercut lateral edges of the dorsal notothyrial platform (the inner socket walls), whereas the outer postero-lateral surfaces of the teeth are obliquely striated by five or six ridges and grooves which articulate with a complementary set developed on the outer socket walls (text-fig. 11d). A low median ridge, posteriorly indented down the middle, extends along the floor of the pedicle valve for about one-third its length and divides a wide, poorly differentiated muscle scar.

The dorsal interior is unique in a number of features (text-fig. 10a-c). The cardinal process stands high above the hinge-line. It consists essentially of a rod of secondary fibrous calcite tapering slightly posteriorly and flattened along its ventral surface where there occurs a pair of deep hollows, elongated with the long axis of the process, and separated from each other by a postero-median ridge (text-fig. 11a). The anterior ends

of the hollows are inserted into the shaft of the process as a pair of short pits directed antero-ventrally, and they must have acted as seats of attachment for the dorsal diductor muscles (text-fig. 11c). The cardinal process is continuous with a well-developed notothyrial platform, which passes anteriorly into a low median ridge, and flares laterally to form the inner walls of elongate sockets disposed obliquely to the hinge-line. The striated outer walls of the sockets also stand above the hinge-line medianly, where they are ankylosed to the dorsal surface of the cardinal process to form a gently arched structure, which is rutted by growth-lines and is seen externally more or less occupying



TEXT-FIG. 11. Ten sections through the shell of *Tropidoleptus carinatus* (Conrad) to show especially the structure of the cardinalia and the brachidial apparatus of the brachial valve.

the delthyrial opening. This structure has previously been referred to as the chilidium, but it is not homologous with that feature as developed in the strophomenoids, because it could only have been deposited by the pediculate-outer epithelial junction; it is thus equivalent to the antigyidium, which is also found in other orthoids like *Hesperorthis* (Williams 1956, p. 258).

The notothyrial platform gives support to a pair of subparallel crura, lanceolate in transverse section, with the sharper edges directed ventrally. In adult shells the crura arise slightly antero-medially of the outer socket walls, but they retain their individuality within the heavy accretion of the notothyrial platform, and can be traced back to the hinge-line, where they become continuous with a pair of slender nodes representing the socket plates of young shells (text-fig. 11d-f). In all three specimens sectioned by us, the crura extend anteriorly for about one-quarter the length of the brachial valve, and then give rise to a pair of short, slightly divergent apophyses (text-fig. 11g). Meanwhile, the low ridge on the floor of the valve passes anteriorly into a high median septum, consisting of a middle plate of prismatic calcite coated by a thin layer of fibrous calcite (text-

fig. 11*h-j*). The septum extends anteriorly for about two-thirds the length of the valve. Posteriorly, it has been appreciably undercut by epithelial resorption to form a posteriorly directed 'median prong', which supports a pair of slender outgrowths. These are plate-like in transverse section, with the long axes normal to the plane of the median septum. Hall and Clarke (1894, p. 305) described specimens in which the apophyses from the crura are continuous with the septal outgrowths, and they concluded that this mode of growth revealed the terebratellaceid affinities of the genus. Such a fusion is not found in the three adult specimens on which this description is based. None the less the arrangement, whether or not it led to the completion of the loop, is remarkable in that the resultant structure is demonstrably composed of two distinct elements in the terebratellaceid fashion.

The development of the dorsal septum now becomes a crucial matter. Its basic structure, the medianly disposed plate of prismatic calcite, can be traced posteriorly along the floor of adult valves, buried beneath the median ridge and the notothyrial platform, to within 1 mm. of the hinge-line, where it stands about 0.5 mm. above the external surface of the brachial valve. The average depth of the pedicle valve is about one-quarter its length, and, when allowance is made for the height of the septum relative to the convexity of the shell, it is evident that, even in specimens a few millimetres long, the septum must have stood as high above the dorsal floor as it does in adults, where it almost divides the brachial cavity into two. In this event, the septum would certainly have intervened between the generative tips of an early schizolophe in the same way as it does in recent terebratellaceids.

The development of a septum among orthoids is not uncommon; it is known, for example, in *Skenidioides*, *Phragmorthis*, *Mystrophora*, *Phragmophora*, &c. But there are two fundamental differences. First, the shells of the four genera just named are very much deeper, and the crural counterparts are directed ventrally rather than anteriorly as in *Tropidoleptus*, so that their lophophore disks may well have been suspended ventro-posteriorly of the septa, and thus may have developed without complications into spirolophes. Secondly, and more importantly, the growth of apophyses anteriorly from the crura must have prevented any lateral migration of the first formed coil of the lophophore, other than the kind of adjustment which would have normally accompanied the growth and resorption of the calcareous supports. Consequently, it seems reasonable to assume that the apophyses and the posteriorly directed outgrowths from the median septum, which arose in the same way as the descending branches of the terebratellaceids, supported the first formed part of the lophophore, and that this was accordingly disposed as an oval broken anteriorly by the septum. In adult shells, however, which attained a width of over 30 mm., proliferation of the lophophore from the paired generative tips almost certainly exceeded the length accommodated by the oval formed of the crural apophyses and the septal outgrowths. Yet the only possible skeletal equivalent to the ascending branches (invariably developed in the terebratellaceids in contrast to the descending ones) is the posterior part of the median prong. The height of the prong above the floor of the brachial valve, together with the shallowness but relatively great width of the shell, suggests that the later formed portions of the *Tropidoleptus* lophophore were arranged in an entirely different way from those of the terebratellaceids. In the initial stages of lophophore development, the generative tips would have been contiguous with the prong and ventral of the outgrowths. But further growth would



necessarily have resulted in a migration of these coiled ends of the lophophore away from the prong, and the proximity of the pedicle valve would have ensured growth towards the lateral areas (text-fig. 10*d, e*).

In retrospect, it seems best, despite the unusualness of the dorsal interior, to accept *Tropidoleptus* as a dalmanellaceid. In respect of the dual origin of the loop, the stock anticipates the development of the descending branches in the brachidial apparatus of the later, unrelated, terebratellaceids, but the disposition of the lophophore in adult *Tropidoleptus* is most likely to have consisted of an oval-shaped, primary coil, supported by extensions from the crura and the median septum, and a pair of unsupported planar or low helicoidal spires, separated from each other by the high dorsal septum, and lying more or less in the plane of the commissure.

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ALWYN WILLIAMS and A. D. WRIGHT  
 Department of Geology,  
 The Queen's University,  
 Belfast.

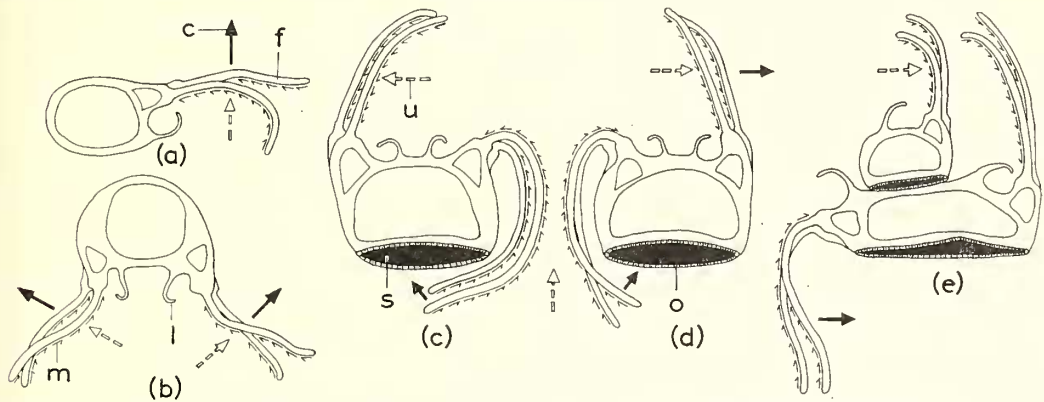
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#### ADDENDUM

*Filter feeding in spire-bearing brachiopods.* Since the submission of this paper, Dr. M. J. S. Rudwick (1960a) has published an interpretation of the feeding mechanism in spire-bearing brachiopods, which involves a refutation of the opinion expressed here to the effect that calcareous spires were equipped with a doubled lophophore, the deutero-lophe. Put very briefly, Rudwick is concerned with the efficiency of the brachiopod filter feeding system in separating filtered, exhalant water from unfiltered, inhalant currents, with the filaments, through which water passes from the frontal surfaces—those facing the lip—to the abfrontal ones, acting in concert like a straining valve (text-fig. 12). The flow of water in an abfrontal direction is normally irreversible except in *Argyrotheca* (Atkins 1960), which anomaly only effects Rudwick's conclusions in so far as the atrypid and spiriferid current systems may have been interchangeable. Using an irreversible model, Rudwick finds that efficient filter systems can be reconstructed for the spire-bearing brachiopods by assuming that the skeleton bore a single series of filaments, which could only have come about if the generative tips of the lophophore migrated away from their median juxtaposition in the trocholophous stage of development, and were, during subsequent growth, coincident with the ends of the epithelial sheaths to the primary spires. This assumption leaves open the function of the jugum and its elaboration into spinose platforms, stems, and coextensive whorls (except possibly as subsidiary supports to the lophophore occupying the primary spires). Rudwick cites the facts that the lophophore and the internal skeleton grow independently of each other and are differently disposed in Recent terebratuloids, to support his belief that the jugum was not important to the attitude of the lophophore. But terebratuloids are not good examples to quote, because, when a median septum and/or a transverse band develop, they do in fact support the generative zones of the lophophore, which may coil in the median plane but never migrate laterally in the manner described by him.

Rudwick has also stated that the best interpretation is one which explains the greatest number of facts (1960b, p. 518). Without being prejudicial to his conclusions, there is

but one fact relevant to this discussion, and that is the existence and persistence of a jugum. Certainly, judging from Recent brachiopods, it is highly likely that the spire-bearers fed by filter systems, which must have worked competently enough to ensure group survival for over 300 million years, although they need not have been as efficient as Rudwick would wish. Further observations of his, like the 'moulding' of the spiralia to the 'form of the mantle cavity' (p. 380), and the 'anterior flaring' of the brachidium to accommodate a 'median exhalant current' (p. 380), are either generalizations or hypotheses and could be used with equal conviction in other reconstructions. In effect, his rejection of the deuterolophe does not spring from a demonstration that its jugal



TEXT-FIG. 12. Transverse sections through the spirolophe of *Tegulorhynchia* (a) and the side arm of *Terebratulina* (b) and the inferred deuterolophe of spiriferoids (c), (d), with accessory calcareous spires (e):—f. filament, l—brachial lip, m—direction of movement of food particles, o—outer epithelium, s—supporting calcareous ribbon, u—unfiltered, inhalant current, c—filtered, exhalant current.

connexions could not have supported the generative parts of the lophophore, but from an opinion that it could not have functioned as a filter system.

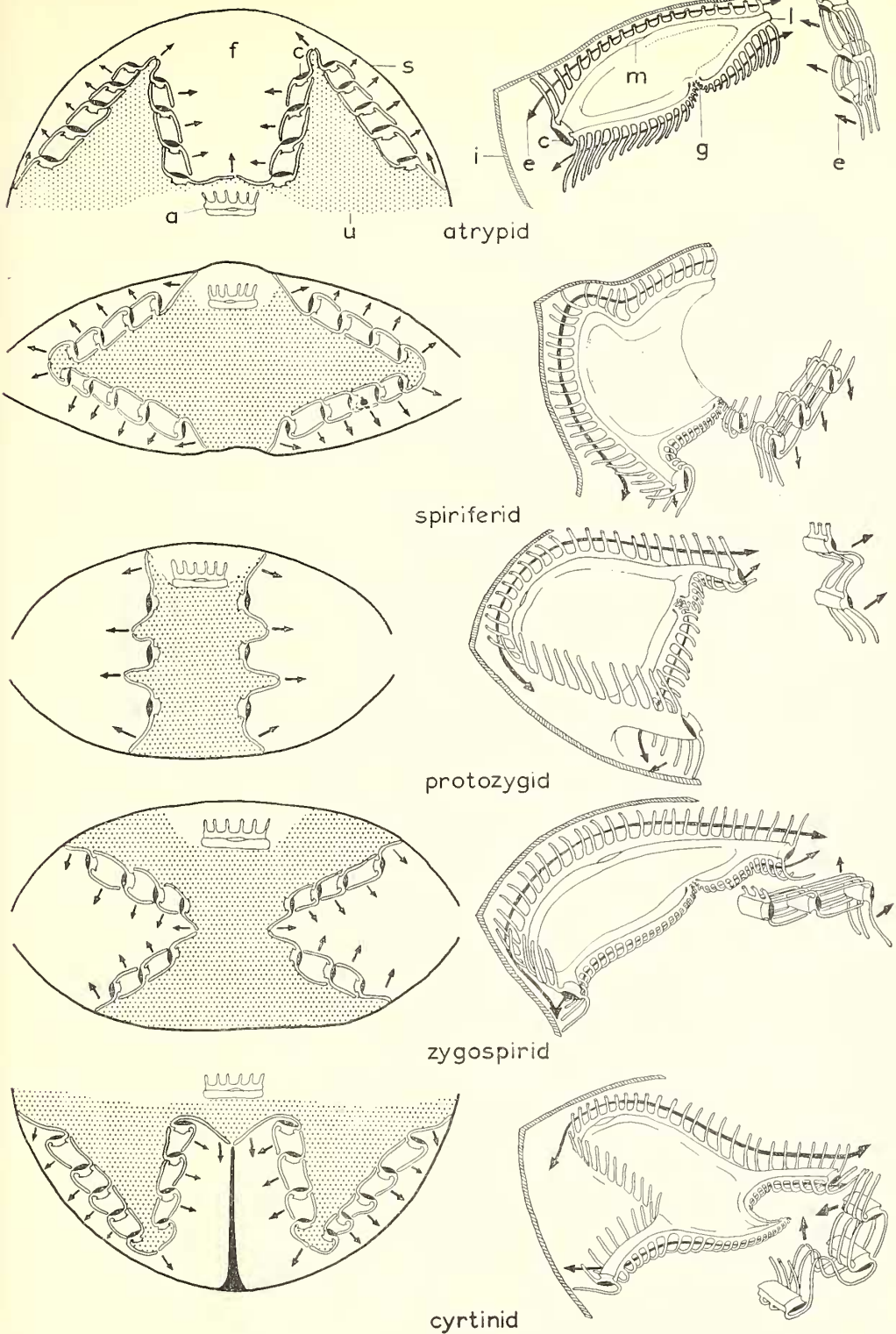
In an exchange of letters about the article, the homology between the plectolophe and the deuterolophe was taken so literally as to envisage each spirally coiled, doubled lophophore acting as a 'filter tube' (comparable with that formed by the contiguous generative zones of the terebratuloids) which was fed by unfiltered water entering ventro-medially, and separated from the filtered water, within and outside the cones, by the lateral filaments of the jugum resting on the ventral walls of the first coils and by the shorter median filaments deflected antero-ventrally (Williams, p. 516). The system was admittedly 'cumbersome' (p. 516), and Rudwick considered it to be hydrodynamically weak (p. 517). At the same time, it was suggested that, if a median exhalant current operated in the spiriferids in the style favoured by Rudwick, only filtered water would have been supplied to the mouth section of the lophophore subtended between the crura. Rudwick countered with the opinion that the filaments would have arched over the lip of this segment to touch the dorsal surface of the inner epithelium, and described the structure as the reverse of the arrangement around the mouth of living rhynchonellids. This is still difficult to visualize, because the rhynchonellid exhalant canal is dorsal of a series of posteriorly deflected filaments belonging to both the mouth segment and the posterior part of the basal coils, which are in the same plane. In Rudwick's spiriferid pattern,



however, filaments of the posterior part of the basal coils would have been deflected posteriorly to receive an inhalant current, while those of the mouth segment would have incurved anteriorly, and in this attitude could only have presented a pair of circular openings to the lateral inhalant streams when the filaments of the posterior part of the second coils were deflected medianly, so that several of them touched the most lateral filaments at either end of the mouth segment.

The canalization of the exhalant current in the mouth segment of rhynchonellids does, however, provide an important model for possible attitudes adopted by a deuterolophe, and, in conjunction with modifications in the performance of the 'filter tube', may be used to demonstrate efficient filter systems of feeding by any type of deuterolophe. Thus, posteriorly deflected filaments of the mouth segment and antero-dorsally deflected filaments of the generative ends of the lophophore situated on the jugum would have touched either the inner epithelium bounding the mantle cavity or connective membranes, known to drape the loop of modern terebratuloids and feasibly inferred to have existed about the jugum of the spire-bearers. In this manner, two streams of filtered water, flowing dorso-laterally, would have been effectively separated from a median, inhalant current. Add to this segregation the possibility of inducing currents to pass from within a cone or from outside it simply by the reversal of oppositely directed filaments on the deuterolophe—text-fig. 12, (c), (d)—and the basic pattern of current systems could have been the same in all spiriferoid brachiopods irrespective of the attitude of the spires.

Rudwick effectively used the presence of spinose outgrowths to determine the position of the lophophore on the calcareous, spiral ribbons, but this procedure is not necessary if the attitudes of the spires are considered relative to the axis of the mouth segment lying between the ends of the crura, where the lip must face ventrally. By this means, all possible attitudes taken up by the lophophore of spire-bearers may be referred to one of five fundamental positions which have been illustrated in text-fig. 13. In the atrypid type, with dorsal directed spires, it is assumed that the inhalant current entered ventro-medianly and passed into the cones while the exhalant canals from the mouth region and the jugum fed dorso-laterally into the exhalant chamber containing the cones. In the spiriferid type a median, inhalant current diverged to pass laterally into the cones, and the exhalant canals from the mouth segment and the jugum entered the separated, exhalant chambers peripheral to the cones. In the protozygid type the plano-spiral deuterolophe effectively sealed off a median, inhalant chamber from a pair of lateral, exhalant ones, each of which was joined dorso-laterally by the exhalant canals of the mouth segment and jugum. The zygospirid arrangement is essentially the same as the protozygid one except that the apices of the cones are directed inwardly, and the median inhalant current became filtered during the passage of water *into* the cones. Finally, for the cyrtinid type with ventrally directed cones, it is assumed that a median inhalant current passed into the cones through a gape, which was created by the inner series of filaments on the anterior part of the basal coils curling outwards to touch the antero-median part of the ventral commissure. The inner filaments of the posterior arcs of the basal coils would then have been outwardly deflected to rest on the dorsal inner epithelium and, together with the exhalant canals of the mouth segment and jugum, would have ejected filtered water postero-laterally; while those along the median parts of the basal coils would have been deflected towards the ventral median septum to form an arch, which would have separated the exhalant chambers containing the cones from the median incoming stream.



TEXT-FIG. 13. Diagrammatic reconstructions of current flow seen transversely (left-hand drawings) and around the mouth segment (right-hand drawings) in five different attitudes of the spiriferoid deutero-lopne: a—stylized mouth segment for orientation of the feeding apparatus, c—calcareous ribbon of spiralia, g—generative zone, i—inner epithelium, l—brachial lip, m—mouth, s—shell, e—exhalant current, f—filtered water, u—unfiltered, inhalant water.

Escape from the exhalant chambers formed in this way would also have occurred postero-laterally.

All these systems are, hydrodynamically, at least as efficient as any described by Rudwick, and, with two series of filaments on each coil setting up a current flow in the same direction, they could have acted as more powerful pumps. Moreover, novel reorientations of the spires would not require a concomitant change in the direction of the inhalant current, which, according to the interpretation given here, was *always* a median one, as it most probably was in the young stage of *all* spire-bearers. Indeed, it might well be argued that the variety of attitudes assumed by the spires in this group of brachiopods was functionally possible because the calcareous ribbons bore, not a simple spiroloph, but a deuteroloph, which, irrespective of its disposition, effectively filtered an invariably median, inhalant current. In this respect, it may be significant that in all but the zygo-spirid system, unfiltered water passed into conical or planar filamentous screens and that the exceptional stocks, in which filtered water occupied the cones, were short-lived, unimportant members of the group. Rudwick (pp. 377, 517) has remarked adversely on the wealth of filaments and the crowding of filter tubes in a deuteroloph, but these cannot be more than minor objections. Reference has been made, in the main article, to the decrease in the number of filaments per unit length of the terebratuloid side arms relative to their incidence near the generative zones, due to the proliferation of non-filamentous tissue. Spiralia, which are known to have been up to ten times as long as the side arms, can be expected to have borne two series of filaments so widely spaced that each set on one whorl would have alternated with sets on adjacent whorls. Nor can crowding between the spiral ribbons be seriously considered as detrimental to the efficient operation of the deuteroloph. Each succeeding whorl must necessarily have a shorter perimeter than the one before, so that whorls of filter tubes mainly occurred within one another from base to apex: and from the example afforded by the *Terebratulina* side arm, where one common canal supported a doubled lip and two filament series—text-fig. 12 (b)—it can be safely inferred that the deuterolophous segments supported by the spires need only be slightly wider than the simple lophophore proposed by Rudwick. In fact, if the accessory spires of stocks like *Diplospirella* supported lophophorous segments which had diverged from the median zone of the jugum, room could even be found for them in the manner illustrated in text-fig. 12 (e).

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